Published online February 6, 2007

Interaction of Plant Species Diversity on Grazing Behavior and Performance of Livestock Grazing Temperate Region Pastures

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ABSTRACT

The importance of plant species diversity on performance of livestock grazing temperate region pastures is summarized in this review. As livestock producers seek less capital-intensive production systems, emphasis is redirected toward low-input pasture systems that rely on complex species mixtures to produce forage. Increased plant species diversity has been linked to improvements in ecosystem function. While it is recognized that grazing management can have a profound impact on sward composition, which in turn can affect grazing behavior and animal performance, the effects of increased plant species diversity on animal productivity (and vice versa) have not been well explored. This review addresses mechanisms by which grazing livestock alter cool-season plant species diversity, mechanisms of diet choice, effects of plant species diversity on animal performance, and implications to sustainable domestic livestock grazing systems. We review evidence for these effects at one trophic level, that of grazing livestock in agroecosystems. While grazing behavior research conducted during the last several decades has led to advances in the understanding of plant–animal interactions, improved knowledge of these interactions is crucial for predicting animal performance. Also important is the evaluation of the impact of grazing livestock on mixed sward dynamics. This knowledge will lead to new opportunities to develop environmentally and economically sustainable grazing systems.

Farmers continually face new challenges in pasture management, such as evolving agrienvironmental schemes to protect natural resources, and therefore need new management techniques to remain sustainable. Increased plant species diversity has been linked to improvements in ecosystem function, including increased primary (plant) productivity, greater stability in response to disturbance, improved nutrient cycling, and greater resistance to weed invasion (Hector et al., 2005; Spehn et al., 2005). These improvements in function could be of great benefit to agriculture (Tilman et al., 1999; Minns et al., 2001). Preliminary research suggests that manipulating plant diversity can improve primary production in grazed systems (Sanderson et al., 2005) and can reduce weed pressure (Tracy and Sanderson, 2004). It is not clear, however, whether the benefits suggested by these limited-scale studies will apply more broadly to managed forage and grazing lands.

Definitions of diversity vary widely, so it is important to establish a common ground when discussing the importance of diversity to ecosystem functioning. Diversity encompasses two concepts, the idea of richness—the number of species present—and evenness—the relative abundance of species present (Magurran, 2004). Species richness is often used as a surrogate for diversity in studies of the diversity–function relationship, but is not a complete measure of the diversity of a community. Two sites with the same number of species can vary widely in their levels of evenness, and thus diversities. For example, one site may be dominated by a single species and the other species are all rare, while the second site has similar abundances of all species present. Species abundances are probably also important to ecosystem function, although this information is often neglected. As used here, diversity refers to taxonomic diversity, the number and abundance of species present; but in other contexts, diversity may describe genetic, functional, or structural variability.

Increasing input costs and volatile prices received for agricultural products have resulted in some dairy and livestock operations opting for low-input pasture systems that rely on complex species mixtures to produce forage (Rotz and Cropper, 1998; Sanderson et al., 2001). While research with clipped plots has shown advantages of increased plant species diversity on forage production (Tracy and Sanderson, 2004; Deak et al., 2004), the effects of increased plant species diversity on secondary (animal) productivity have not yet been well explored. Factors such as species richness, sward patchiness, and individual species distribution and their effects on animal grazing behavior and resulting performance remain a subject of debate. Much of the research to date has been conducted using either monocultures or simple two-species mixtures of one legume and one grass species. The effects of complex mixtures (i.e., mixtures of several grasses, legumes, and forbs) on animal performance (and vice versa) are still relatively unknown. Improved knowledge of plant–animal interactions is crucial for predicting diet selection, intake, and performance of grazing animals on complex mixtures, as well as evaluating the impact of grazing livestock on the dynamics of mixed swards. In this paper, we summarize the current knowledge on plant species diversity and performance of livestock grazing temperate region pastures. We discuss mechanisms by which grazing animals alter plant species diversity, mechanisms of diet choice, effects of plant species diversity on animal performance, and implications to sustainable domestic livestock grazing systems.

IMPORTANCE OF PLANT SPECIES DIVERSITY IN PASTURES: A PLANT-BASED VIEW

The role of plant species diversity in pastures, mainly from a plant and soil viewpoint, was reviewed by Sanderson

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Published in Crop Sci. 47:416–425 (2007).
Symposia
doi:10.2135/cropsci2006.01.0061

et al. (2004). Close scrutiny of many temperate-region pastures reveals a rich tapestry of plant species in the sod. Surveys of pastures in the northeastern USA show a wide range of plant species richness at the plant community, pasture, farm, and regional scales (Tracy and Sanderson, 2000). Generally, biodiversity in grasslands decreases as management input intensity increases (Tallowin et al., 2005).

Pastures can be very diverse ecosystems, but many components of this biodiversity cannot be easily managed or directly manipulated for production purposes. Plant species diversity, however, may be the component of biodiversity most amenable to management. The question remains, however, as to whether increasing the botanical complexity of mixed swards would be beneficial to producers in terms of herbage or animal production, stability, or uniformity of production.

Herbage Production

One of the principal benefits ascribed to increased plant diversity in grassland systems has been increased primary productivity (i.e., herbage yield). Higher herbage yield at higher species diversity has been attributed to the ability of a mixture containing many species to use resources more completely than a mixture containing fewer species (Hector et al., 2005; Hooper et al., 2005). Early applied research on complex forage mixtures in the USA documented either no significant trend in herbage yield with increasing seeded species richness (Brown and Munsell, 1936) or a positive relationship between herbage yield and seeded species richness (Bateman and Keller, 1956). Washko et al. (1974) reported a weak positive relationship between herbage yield and mixture complexity (seeded species richness) at one Pennsylvania location and no relation at another location. In all of these studies, the species composition of the mixtures had as much or more effect on herbage production than did the number of species sown.

Small-plot studies in England (Bullock et al., 2001), New Zealand (Daly et al., 1996), and the USA (Deak et al., 2004) have shown improved herbage production with mixed swards of several grasses, legumes, and forbs. In certain instances, the increased herbage production resulted from greater summer growth of the legume and forb components. Two pasture-scale studies in the USA indicated a benefit in herbage production for complex mixed swards compared with a simple grass–legume mixture (Sanderson et al., 2005; Skinner et al., 2006). In both studies, the yield benefit resulted mainly from including highly productive, drought-tolerant species (e.g., chicory, *Cichorium intybus* L., and alfalfa, *Medicago sativa* L.). A major disadvantage reported in the small-plot and pasture-scale studies was that nearly one-half of the planted species in the complex swards did not persist beyond 3 of 4 yr., indicating that species presence was not very stable in these mixtures.

Other field-plot studies have shown no benefit to forage production from highly complex forage mixtures (Zannone et al., 1983) and studies in the New Zealand hill country reported inconsistent evidence of production responses to forage species richness (Scott, 2001; Dodd et al., 2003; White et al., 2004).

Ecosystem Stability

Another tenet of plant biodiversity theory is that increased diversity contributes to the stability of ecosystems. Here the rationale is that with higher species diversity, there is a greater likelihood of some species prospering under all conditions, so that there is always some production (the insurance hypothesis; Yachi and Loreau, 1999; Fridley, 2001). In a small-plot study, mixtures of up to 15 species of legumes, forbs, and grasses did not improve forage yield or yield stability (Tracy and Sanderson, 2004). Most of the mixtures decreased in species number during the 3-yr study and became dominated by perennial grasses.

Research on New Zealand high-country grazing lands showed that species richness and evenness were weakly associated with the stability of sheep (*Ovis aries* L.) production as measured by the coefficient of variation in annual carrying capacity (Scott, 2001). Stability of temperate grazing lands in southern Australia was not related to species richness (Kemp et al., 2003). New Zealand researchers reported a high coefficient of variation for low numbers of species, and a decreasing coefficient of variation as species number increased; evidence of reduced risk from species-rich grasslands (Nicholas et al., 1997).

Weed Invasion

Greater plant diversity in grassland ecosystems may contribute to resistance to invasion by weeds and pests by using resources completely, leaving no space for weed species to become established and thrive (Tilman, 1997; Kennedy et al., 2002). Weed abundance decreased in experimental pasture mixtures as the evenness of forage species increased (Tracy and Sanderson, 2004). In addition, species composition of the mixture affected weed abundance: mixtures based on tall fescue (*Festuca arundinacea* Schreb.) had fewer weeds in the soil seed bank and aboveground vegetation than did mixtures based on smooth bromegrass (*Bromus inermis* Leyss). Similar results were found in a series of greenhouse, field, and survey experiments with cool-season pasture species in the northeastern USA (Tracy et al., 2004). Weedy species were less abundant in pastures sown to complex mixtures of grasses, legumes, and forbs than in simple grass–legume mixtures (Sanderson et al., 2005). However, weed abundance in New Zealand pastures decreased as the number of plant functional groups (sets of plant species showing similar responses to the environment and similar effects on ecosystem functioning; Gitay and Noble, 1997) in the pasture increased (Dodd et al., 2003).

Although many areas remain where further research is needed, the literature supports the view that primary productivity and invasibility are affected by higher plant diversity. However, all ecosystems comprise complex food webs that involve organisms at many trophic levels, so it follows logically to propose the hypothesis that diversity at the primary level may affect ecosystem function at these other levels (Hooper et al., 2005). The remainder of this paper reviews the evidence for effects at one trophic level, that of grazing livestock in agroecosystems.

BEYOND THE PLANT: GRAZING ANIMALS AND DIVERSE SWARDS

Grazing animals play a key role in altering plant species diversity in grass lands (Rook and Tallowin, 2003); however, little research has evaluated the effects of plant species diversity on animal performance. Of the few studies available, nearly all are limited to simple 1 grass–1 legume mixtures, with contradictory results in dairy cattle (*Bos taurus* L.) (Wedin et al., 1965; Harris et al., 1997; Phillips and James, 1998; Rutter et al., 2004) and sheep (del Pozo et al., 1997; Wright et al., 2001). Evaluation of more complex forage mixtures on animal performance has not been thoroughly evaluated and must be considered to develop sustainable grazing systems. In this section, we explore the grazing animal–sward interaction relative to plant diversity.

Species Richness in Relation to Herbivory

The relationship between grazing and species richness is complex and nonlinear (Olff and Ritchie, 1998). Low to moderate levels of grazing pressure opens the canopy allowing more light penetration of the sward and permitting minor species to flourish, resulting in increased species richness and diversity of the sward. Intense grazing pressure reduces species richness by eliminating the less-grazing-tolerant species. This is consistent with the prediction of the intermediate disturbance hypothesis, which suggests that species diversity will be highest at moderate levels of disturbance (Connell, 1978). Although grazing is a planned part of the system, from the plant perspective it is a disturbance since grazing removes biomass.

The positive effect of moderate grazing on diversity has been used to help restore species-rich northern European grasslands (Pykala, 2003). The oldest continuously grazed plots had the highest species richness, and grazing showed promise as a method for restoring high diversity to abandoned pastures. The greatest diversity, however, may only be achieved at grazing intensities less than usually practiced. This indicates that plant diversity must be balanced against other agricultural and economic goals (Tallowin et al., 2005).

Mechanism by which the Grazing Animal Alters Sward Plant Species Diversity

Plants exhibit a range of defensive responses to defoliation. In particular, defoliation can lead to miniaturization of leaves and the adoption of a more prostrate growth habit (Parsons and Chapman, 2000). Mechanisms by which defoliation can alter the competitive advantage between plant species include direct removal of phytomass by altering the light environment (Bullock and Marriott, 2000; Olff and Ritchie, 1998) and by nutrient uptake. In the case of regularly mowing the species, species composition can be very different to one that is infrequently mown. Indeed, regular mowing (frequent grazing and periodic mowing) is essential to the maintenance of most grasslands, at least in temperate regions, which would otherwise success to scrub and ultimately to forest.

Unlike mowing, defoliation by animals is selective, both between plant parts and between different plant species (Bullock and Marriott, 2000). This selectivity creates additional structural heterogeneity in grazed as compared with mown swards with some areas being intensively and repeatedly grazed and others being grazed only infrequently with consequent changes in plant morphology as outlined above. This creates different microhabitats and can result in a greater range of species surviving in the same area.

Heterogeneity resulting from grazing can occur at a range of scales. At the small scale of the individual bite or feeding station, heterogeneity can be driven either by feedback effects from initially random defoliation or by the initial occurrence of aggregation of preferred species. There have been several studies of animal movements at this scale in simple model systems (Roguet et al., 1998; Rook et al., 2004a) and this information has been used in mathematical models of foraging movements (Baumont et al., 2002) that provide a sound basis for generalization to more diverse systems. At a larger scale, choice of grazing location may also be driven by factors other than food, such as water, shelter, and social cohesion (Dumont and Boissy, 2000) and attempts have been made to include these in models (Beecham and Farnsworth, 1998; Pérochon et al., 2001).

Selective defoliation is not the only mechanism by which grazing animals affect sward heterogeneity. Physical damage to swards by treading can affect microhydrology, which can provide opportunities for the establishment or competitive advantages for a different suite of plants (Bullock and Marriott, 2000). Where treading opens up bare soil it provides regeneration niches for gap-colonizing (ruderal) species that would not otherwise be able to coexist with perennials that are more competitive (Bullock and Marriott, 2000).

A third mechanism acting to increase heterogeneity in grazed swards is nutrient cycling through the animal. This has the effect of concentrating nutrients at dung and urine patches and again may alter the local competitive advantage between species, both directly and by feedback effects on dietary choice, as, at low stocking rates, cattle in particular will not graze near dung patches (Bokdam, 2001).

Grazing animals can also have a more direct effect on the presence or absence of species in a sward via their role in seed dispersal. This can be either endozoochorus (i.e., by seeds passing through the animal's digestive system) or exozoochorous (i.e., by seeds attaching to the animal's coat) dispersal (Bakker, 1998).

The relative importance of these mechanisms for creating heterogeneity will depend on the particular type of grassland and the management goals for that grassland. For example, in communities that are already diverse, the balance between species may depend mainly on the effects of animals' dietary choices whereas treading may have a particularly important role in allowing species colonization of grasslands undergoing extensification. The relative importance of the mechanisms will also interact with grazing pressure. At moderate grazing pressure, animals are more able to express their dietary preferences and thus this mechanism can be more important and can often lead to maximum plant species diversity levels (Milne and Osoro, 1997). However, if grazing pressure is too low, competitive species may dominate (Tallowin et al., 2005).

Mechanisms of Dietary Choice

Grazing ruminants offered a free choice consume a mixed diet, showing partial preferences for certain forages (Parsons et al., 1994; Hester et al., 1999; Rutter et al., 2004). When offered adjacent monocultures of perennial ryegrass (*Lolium perenne* L.) and white clover (*Trifolium repens* L.) of varying proportions, cows and sheep have consistently selected a diet containing ≈70% white clover (Parsons et al., 1994; Rutter et al., 1997a; Rutter et al., 2004). If the main goal of the grazer was to maximize intake rate, as predicted by the classical foraging theory, these animals should have consumed 100% clover (Rutter et al., 2004), but this was not the case. Domestic sheep and wild red deer (*Cervus elaphus* L.) exhibited a preference for grass (primarily *Agrostis* spp. (60%), *Deschampsia flexuosa* (20%), *Festuca* spp., and a range of forbs) over heather (*Calluna vulgaris* L. Hull) in that they spent 50% of their time on grass while the grass only constituted 15% of the area of each plot (Hester et al., 1999). While grazing the grass patches, both sheep and red deer moved more slowly, had longer grazing bouts, and had faster bite rates than on heather. It is not yet clear why grazing livestock select mixed diets. Several possible explanations have been suggested, including (i) grazing animals are trying to match the ratio of reward rates with the ratio of food types in the diet (Senft et al., 1987), (ii) discrimination error (Illius et al., 1999), (iii) the need to maintain effective rumen function (Rutter et al., 2000), and (iv) perceived risk of predation which influences diurnal patterns of preference (Newman et al., 1995).

In these experimental conditions, the animals were subjected to minimal physical constraints to selection and could therefore express unconstrained preference (Hodgson, 1979). The animals can maintain their preferred dietary composition despite changes in the proportional area of the two species offered (Newman et al., 1992; Parsons et al., 1994; Rutter et al., 1997a). However, in reality, grazing animals are presented with challenges with mixed swards (aggregation, vertical and horizontal differences, availability of different species, etc.) in seeking out the preferred diet, which can have a significant impact on time spent grazing and dry matter intake (Rook et al., 2002). Most reported studies were short-term, frequently only a few weeks (or hours) in length with a handful of actual collection periods within this time frame. There are fewer data on dietary choices over the long term. However, it has been shown that preferences can change based on the changing dynamics of the sward structure and nutritional status of the animal (Rook et al., 2002).

Biting Behavior and Patch Choices

Diet selection can be affected by patch size (WallisDeVries et al., 1999) and, more generally, the spatial distribution of preferred food patches (Dumont et al., 2000). Animal selectivity is greater when preferred patches are aggregated as opposed to randomly dispersed across the landscape (Dumont et al., 2002). Rook et al. (2004b) suggested that there is a trade-off between the benefits of eating a preferred food and the costs of foraging for that food; the costs of searching for patches is increased when they are dispersed. This could have profound implications in predicting local extinction risk of environmentally important or endangered plant species according to its feed value and within-plot distribution, and to lead to a definition of appropriate grazing management strategies to ensure the plant's conservation (Rook et al., 2004b).

Balancing Digestive and Time Constraints

Grazing animals must satisfy daily nutritional needs in the time they can spend grazing (Baumont et al., 2005). Short-term feed preferences are modulated by the regulation of diet choice and intake, which integrate digestive and nutritional feedbacks; this in turn governs the balance between motivation to eat and satiety (Baumont et al., 2000). In the longer term, the time scale also incorporates behavioral compensatory mechanisms incorporating travel speed between patches, biting rate, and grazing time (Baumont et al., 2005).

Digestible organic matter intake may be considered as a currency that grazing ruminants maximize because digestible organic matter intake integrates both quality and quantity of food ingested. This is attributed to a wide range of theoretically possible strategies from maximizing quality to maximizing quantity (Baumont et al., 2005). Greater selective behavior occurs when grazing animals seek out parts of plants or patches of high digestibility that are frequently lower in accessibility. This would increase grazing time while decreasing intake rate. Less selective behavior would occur when maximizing quantity. The link between behavioral and digestive constraints must consider the trade-off between quantity and quality (Baumont et al., 1990).

Ruminants will increase grazing time to adapt to a decrease in forage availability (Allden and Whittaker, 1970; Penning et al., 1991; Rook et al., 1994a). Cattle and sheep have been shown to increase grazing time on a preferred sward as its accessibility decreases while a lower quality alternative was simultaneously offered (Hester et al., 1999; Rook et al., 2002; Ginane et al., 2003). Sheep will actively attempt to maintain their dietary preference for clover (compared with perennial ryegrass) by increasing grazing time spent on the clover, despite the need to graze for much longer on account of the reduced intake rate on clover as sward height decreased under continuous grazing (Rook et al., 2002). Sheep have also been shown to have lower intake but greater grazing time on mixed ryegrass–white clover swards compared with when the two species are offered as adjacent monocultures. This is due to the need to spend more time searching for the preferred dietary component in a mixed sward (Champion et al., 2004). However, there are limitations on how much grazing time can be increased to meet nutrient demands, especially for animals with high nutritional requirements (Gibb et al., 1999). Additionally, since digestive regulation limits high intakes of highly indigestible material, animals are most likely to trade off and ingest both alternatives (higher and lower digestibility forages), resulting in a mixed diet (Baumont et al., 2005). Grazing time was similar in cattle when timothy (*Phleum pratense* L.) was added to a perennial ryegrass sward (Phillips et al., 1999). However, when orchardgrass (*Dactylis glomerata* L.) as well as timothy were introduced to the perennial ryegrass sward, cattle increased their grazing time compared with a perennial-ryegrass-only sward. Cattle grazed the orchardgrass subplots longer than the perennial ryegrass and timothy, and they also ruminated longer, suggesting their intake of fibrous material was increased (Balch, 1971). This behavior also suggests that the cattle may have been more selective on the orchardgrass plots, spending more time seeking out the higher quality forage.

The diet consumed during the previous meal can have an influence on preference of the subsequent meal. Sheep that had recently grazed grass preferred clover, while those that had recently grazed clover preferred grass (Newman et al., 1992; Parsons et al., 1994). Newman et al. (1992) suggested that these observations were consistent with several alternative hypotheses: a desire for a balanced diet, a response to novelty, or a preference for rarity (Tuttle et al., 1990).

Optimizing Spatial Utilization

As animals search for the best tradeoff between intake quantity and quality, they will repeatedly forage over an area where successful grazing occurred previously. It has been hypothesized that when animals detect sward heterogeneity, their foraging walks are not random, but are structured to efficiently utilize the sward structure (Baumont et al., 2005; Parsons and Dumont, 2003). Cattle and sheep have been shown to have spatial memory of pastures in that intake rate increases as they learn and return to locations where food was previously found, which results in greater foraging efficiency (Dumont and Petit, 1998; Laca, 1998; Rook et al., 2005). Sheep, which graze more selectively than cattle, were shown to have shorter grazing bouts than cattle and lower number of bites per feeding station (Rook et al., 2004a). This may be an adapted behavioral pattern that evolved in sheep to move on more quickly in search of higher quality forage, even when grazing homogeneous swards in which they had no previous knowledge.

Consequences on Sward Dynamics

Selective grazing behavior affects the severity and frequency of defoliation on patches, thereby affecting the quality and quantity of biomass that results from post-grazing growth (Baumont et al., 2005). Repeated defoliation of patches results in a more immature state, with more leaves, less stems, less senescent material, and increased digestibility (Donkor et al., 2003). This may result in a positive feedback relationship between patch grazing and forage quality (Adler et al., 2001), which may in turn promote the continued use of previously grazed patches (Baumont et al., 2005). However, negative feedback may also occur in the animal as long-term patch grazing that may cause changes in plant composition by decreasing desirable species and increasing less desirable species (Baumont et al., 2005). While there is evidence that grazing does affect sward diversity, it is not clear what specific factors (spatial patterns, etc.) drive this effect (Baumont et al., 2005).

Mixed Grazing of Livestock Species and Sward Diversity

Species of grazer can influence sward structure as a consequence of differences in grazing behavior and diet selection. For example, swards increase in white clover content when grazed by cattle compared with sheep (Alder et al., 1967; Briseno de La Hoz and Wilman, 1981). Lambs had greater liveweight gains when grazing ryegrass–white clover pastures that had been previously grazed by goats (*Capra* spp.) when compared with similar swards that were initially grazed by sheep then regrazed by lambs (del Pozo et al., 1996). There was a higher clover content in the regrowth of pastures that were grazed by goats when compared with sheep during the initial grazing period. Bown et al. (1989) supported these findings with observations of increased clover in goat-grazed swards, while swards grazed by cattle or sheep decrease in clover content. Sheep select a diet with a higher proportion of clover than goats (Clark et al., 1982; Radcliffe and Francis, 1988; Collins, 1989), which is probably a function of the mechanics of their grazing behavior in relation to sward canopy structure, as well as active selection (Milne et al., 1982; Penning et al., 1995; Wright et al., 2001).

Grazing of one livestock species can influence the sward structure and botanical composition and provide benefits to (or facilitate) other grazing livestock species. For example, in natural ecosystems, wildebeest (*Connochaetes taurinus albojubatus* Thomas) create ‘lawns’ of short vegetation that subsequently facilitate Thomson’s gazelles (*Gazella thomsonii* Gunther) by providing a dense, vegetative, highly digestible sward (McNaughton, 1976). Facilitation can also occur by grazing with different livestock species simultaneously. Greater output of animal products have been reported when cattle and sheep are grazed together (Nicol and Collins, 1986; Wright and Connolly, 1995; Nicol et al., 2005). Among other benefits, mixed-species grazing resulted in higher intake of stem by cattle (Nicol and Collins, 1986) and grazing of taller vegetation around cattle dung pats by sheep (de Rancourt et al., 1980). In other mixed-species grazing research, combining cows and calves with ewes and lambs resulted in earlier weaning, increased lamb performance, and greater body weight of ewes, but did not affect animal production per hectare (Abaye et al., 1994). Pastures grazed by sheep or sheep and cattle had more Kentucky bluegrass and less white clover and forbs in the sward than pastures grazed by cattle alone (Abaye et al., 1997).

Higher in vitro dry matter digestibilities of pasture were reported for sheep and goats than for cattle, especially when sheep and goats were grazed together with cattle, most likely reflecting their ability (due to smaller incisor arcade breadth and prehensile lips) to exploit their dietary preferences (Nicol et al., 2005). Conversely, pasture dry matter digestibilities were reduced for cattle when grazed with sheep, suggesting that the quality of the diet the cattle were able to select from the available forage was reduced due to competition with the sheep.

The mechanism by which a higher proportion of white clover develops when swards are grazed by mixed livestock species has yet to be determined. Cattle grazing has resulted in higher proportions of white clover irrespective of sward height (Wright et al., 2001). Del Pozo et al. (1996) postulated that goats take shallower bites from the sward surface than do sheep and do not penetrate into the layer of clover lamina, resulting in higher proportions of clover in swards grazed by goats. This mechanism, however, seems unlikely for cattle, for cattle have larger buccal cavities and the resulting bite depth of cattle tends to be greater than sheep (Milne et al., 1982; Laca and Unger, 1992).

Livestock Performance and Sward Diversity

Although numerous studies exist on the effects of sward attributes on bite mass and intake rate of grazing cattle, including sward surface height (Wade et al., 1989; Laca et al., 1994; Rook et al., 1994b) and sward bulk density (Laca et al., 1994), few have examined the effect of plant species diversity on animal performance. Those that have, examined the effect of simple two-species mixtures consisting of one grass and one legume. For example, in what could be regarded as a study of evenness albeit with only two species, lactating dairy cows offered grass pastures containing 25, 50, or 75% clover increased DM intake by 8, 23, and 30%, respectively, when compared with cows grazing a grass monoculture (Harris et al., 1997). Daily milk production for the cows grazing the 50 and 75% clover was similar, and was 33% higher than milk yields for the grass monoculture. Cattle grazing the 75% clover swards may have incurred a protein penalty (i.e., incurred an extra energy cost to metabolize excess protein in the legume-dominant sward) explaining, in part, why milk production responses to increased clover content were nonlinear. A similar study (Yarrow and Penning, 2001) in which perennial ryegrass–white clover swards were managed to produce different clover proportions and then continuously stocked with beef cattle, also showed animal responses to clover proportion but differences were difficult to maintain as under common management all swards converged to have the same proportion of clover.

Grazing research with lactating dairy cows in the mid-1960s indicated that there was no benefit in milk production to planting a complex mixture of grasses and legumes for grazing (Table 1; Wedin et al., 1965). In another study, cows that grazed a mixed sward of white clover and perennial ryegrass had greater (22.1 kg cow^{-1} d^{-1}) milk production than cows that grazed a ryegrass monoculture (18.9 kg cow^{-1} d^{-1}; Phillips and James, 1998). However, when offered a choice of the perennial ryegrass monoculture and the mixed sward of white clover and perennial ryegrass, cows failed to completely select a diet that supported higher milk production (20.0 kg cow^{-1} d^{-1}). The tendency for longer grazing times and the lower stocking rates of the cows in the choice treatment suggests that utilization of the pastures may have been less efficient than for the other treatments (Phillips and James, 1998).

Recent research conducted in a rotational dairy grazing system with a range of swards of different species richness, from a simple orchardgrass–white clover mixture to a complex sward containing nine species (grasses, legumes, and chicory, Table 2; Sanderson et al., 2004; Soder et al., 2006), showed several important trends. First, forage production per hectare as assessed by grazing (with mechanical clipping of excess growth when necessary) did not differ significantly between three, six, and nine species swards but was significantly greater (58%) for these swards compared with the simple two-species grass–legume mixture during a dry year (2002) but not during a wet year (2003; 12% difference). Second, milk produced per hectare did not differ significantly between three, six, or nine species swards but was 86% higher for these swards than for the simple

Table 1. Milk production of dairy cows grazing N-fertilized grass or two grass–legume mixtures in Minnesota (cited in Sanderson et al., 2004, and adapted from Wedin et al., 1965).

Treatment	Carrying capacity	Milk production	
	Animal days ha^{-1}	kg cow^{-1} d^{-1}	kg ha^{-1}
Grass + N†	325	17.1	4733
Simple mixture‡	300	16.8	4233
Complex mixture§	301	15.8	3789

† Smooth bromegrass and orchardgrass received 450 kg N ha^{-1} yr^{-1} in three applications during Year 1 and 235 kg ha^{-1} yr^{-1} in two applications during Year 2.
‡ Alfalfa, white clover, smooth bromegrass, and orchardgrass.
§ Alfalfa, red clover, alsike clover, white clover, smooth bromegrass, orchardgrass, timothy, meadow fescue, and reed canarygrass.

Table 2. Milk production, herbage intake, and herbage yield of dairy cows grazing four different species mixtures at University Park, PA. Adapted from Sanderson et al. (2005) and Soder et al. (2006).

Forage mixture†	Milk yield‡	Herbage intake‡	Herbage yield§ 2002	Herbage yield§ 2003	Milk 2002	Milk 2003
	—kg cow^{-1} d^{-1}—		-kg DM ha^{-1}-		—kg ha^{-1}—	
Two species	34.1	12.9	4800	9000	3885	6676
Three species	35.3	12.1	7400	9900	6957	8871
Six species	34.4	12.1	7900	11300	7486	9821
Nine species	34.3	11.6	7500	9000	7288	8261

† Two-species mixture = orchardgrass and white clover; three-species mixture = orchardgrass, white clover, and chicory; six species mixture = orchardgrass, red clover, chicory, tall fescue, Kentucky bluegrass, and birdsfoot trefoil; nine-species mixture = orchardgrass, red clover, chicory, tall fescue, Kentucky bluegrass, birdsfoot trefoil, perennial ryegrass, alfalfa and white clover.
‡ Data are means of four grazing periods in each of 2 yr.
§ Data are grazing season (April to October) means of two pasture replicates.

orchardgrass–white clover mixture during 2002, a drought year, and 34% higher during 2003, a wetter year. These differences in milk production per hectare arose from differences in stocking rates rather than from daily milk production per cow, which did not differ significantly across the treatments. This lack of per cow effects on milk yield were reflected in the lack of differences in ingestive grazing behavior (grazing time, biting rate, and grazing jaw movements measured using the procedures of Rutter et al., 1997b) and herbage intake (Table 2, Table 3). This is surprising in view of the more mechanistic studies of foraging behavior discussed above. One possible explanation is that these lactating animals had a high intake drive, which made them less selective (Rutter et al., 1997a).

IMPLICATIONS TO LIVESTOCK GRAZING SYSTEMS

Research on the functionality of increased biodiversity in livestock grazing systems is still at an early stage and caution needs to be exercised in making practical recommendations to farmers. There is some evidence that, in low-input grazing systems, increased plant species diversity can improve primary production and reduce weed invasion and also improve system resilience to climatic extremes such as drought (Skinner et al., 2004; Sanderson et al., 2005). These are clearly important considerations for farmers. There is also some evidence that where improvements in primary production are observed, it is reflected in greater total animal production per hectare which is clearly of benefit to producers. However, the costs of using more diverse pastures and their sustainability in the longer term must be taken into account. The effects of greater diversity at an individual animal level are more equivocal and further research is needed in this area. There is also a need for more study of the interaction between greater diversity effects and sward type and animal management regimes.

Table 3. Grazing behavior data for dairy cows grazing four forage mixtures during 2002 and 2003 at University Park, PA. Data are averages of four grazing periods in each year.

	Forage mixture†					
	Two species	Three species	Six species	Nine species	SEM	*P* value
Grazing time (GT), min d^{-1}	421	394	412	401	19	0.3714
GT a.m., min	220	206	201	207	14	0.3315
GT p.m., min	201	188	211	194	14	0.3315
Total bites, bites d^{-1}	19 924	20 066	21 629	21 259	1 380	0.7561
Bites a.m.	10 381	10 788	10 310	10 698	890	0.8164
Bites p.m.	9 543	9 278	11 319	10 561	890	0.8164
Total chews, chews d^{-1}	30 446	28 336	31 781	27 827	1 426	0.1107
Chews a.m.	12 575	11 560	12 405	11 408	1 189	0.9141
Chews p.m.	17 871	16 776	19 376	16 419	1 189	0.9141
Total grazing jaw movements (GJM)	50 170	48 402	53 410	49 086	2 280	0.4589
GJM a.m.	22 756	22 348	22 715	22 106	1 780	0.9005
GJM p.m.	27 414	26 054	30 695	26 980	1 780	0.9005
Bite rate (BR), bites min^{-1}	47	51	52	53	4	0.3976
BR a.m. bites min^{-1}	47	52	51	52	4	0.4356
BR p.m., bites min^{-1}	47	49	54	54	4	0.4356

† Two-species mixture = orchardgrass and white clover; three-species mixture = orchardgrass, white clover, and chicory; six species mixture = orchardgrass, red clover, chicory, tall fescue, Kentucky bluegrass, and birdsfoot trefoil; nine-species mixture = orchardgrass, red clover, chicory, tall fescue, Kentucky bluegrass, birdsfoot trefoil, perennial ryegrass, alfalfa and white clover.

The key to creating and maintaining both desired pasture diversity and optimum animal performance is an understanding of the interactions between grazed plants and grazing animals. Grazing behavior research conducted during the last several decades has led to major advances in the understanding of plant–animal interactions. However, most of this research has been conducted either with monocultures of a limited range of species or simple two-species swards with the unspoken assumption, in many cases, that results could be extrapolated across plant species at a plant functional group level. It is now necessary to understand how characteristics of a wider range of individual species present in these mixed swards affect foraging behavior of the grazing animal, and how the resultant grazing behavior affects sward production and diversity. There is also a need to reexamine the traditional definition of plant functional groups, which in the past have generally been based on the functionality of the plant within the plant community and have taken little account of their functionality with respect to the foraging animals.

CONCLUSIONS

This review has demonstrated that while biodiversity has been shown in many circumstances to improve the net primary (plant) productivity of grazed ecosystems, there has been less evidence that this effect is carried through to secondary (animal) productivity. The limited evidence suggests that, at least under some circumstances, positive effects can be obtained. Given the current cost pressures on temperate animal production systems worldwide and the increasing need for these systems to deliver multifunctional objectives including biodiversity, we conclude that this is an area that merits further research to deliver robust production systems that meet these goals.

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